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PALAEOSPINAX PINNAI N.SP., A NEW PALAEOSPINACID SHARK FROM THE SINEMURIAN (LOWER JURASSIC) OF OSTENO (LOMBARDY, ITALY) (*)

Abstract. — *Palaeospinax pinnai* sp. nov., is described from associated teeth and dermal denticles recovered from the spongolithic micrites of the Lombardische Kieselkalk Formation (Lower Sinemurian, Lower Jurassic) recently excavated at Osteno, northern Italy. The teeth are large (up to 7 mm long) and possess slender upright cusps with coronal ornament restricted to the lateral cusplet pairs. This record adds to the known diversity of the palaeospinacid lineage, and extends the known palaeogeographic distribution of the genus.

Riassunto. — *Un nuovo squalo palaeospinacide del Giurassico italiano.*

Viene descritta la nuova specie *Palaeospinax pinnai*, sulla base di denti e di dentelli dermici ritrovati nella micrite spongolitica della formazione del Lombardische Kieselkalk (Sinemuriano inferiore, Giurassico inferiore) recentemente scavata a Osteno, Nord Italia. I denti sono grandi (lunghi fino a 7 mm) e posseggono sottili cuspidi diritte con ornamenti coronali limitati alla coppia di piccole cuspidi laterali. Questo ritrovamento amplia il quadro complessivo dei palaeospinacidi e la distribuzione paleogeografica del genere.

1. - Introduction.

The fossiliferous deposits of Osteno comprise a four m sequence of non-stratified grey spongolithic micrites within the Sinemurian Lombardische Kieselkalk Formation of the Jurassic (PINNA, 1985). After discovery in quarries along the shore of Lake Lugano in 1964, the deposit was subsequently excavated by the Museo Civico di Storia naturale in Milan during 1980. A moderately diverse invertebrate fauna is accompanied by plants and fossil fishes. The fauna is briefly reviewed by PINNA (1985). It includes a variety of decapod (PINNA 1985), hoplocarid

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(PINNA 1985) and thylacocephalan crustaceans (ARDUINI, PINNA & TERUZZI 1980, 1984; PINNA, ARDUINI, PESARINI & TERUZZI 1982, 1984, 1985; ROLFE 1985); coleoid (PINNA 1972) and ammonoid (PINNA 1985) cephalopods; one enteropneust (ARDUINI, PINNA & TERUZZI 1981); polychaete (ARDUINI, PINNA & TERUZZI 1982) and nematode worms (ARDUINI, PINNA & TERUZZI 1983); ophiuroid echinoderms; bivalves; brachiopods (PINNA 1985), and a variety of land plants (including horsetails, cycads and conifers; BONCI & VANUCCI, 1986).

The fishes have been made available to the British Museum (Natural History) through the kindness of Professor Pinna and his colleagues. They are currently being studied by Drs. Colin Patterson, Brian Gardiner, Peter Forey and Christopher Duffin. The material includes one beautiful specimen of the problematic holocephalan, *Squaloraja* (ARDUINI, PINNA & TERUZZI 1982: 521, pl. 8), a poorly preserved skull of a myriacanthid holocephalan, a variety of actinopterygians, and some coelacanthid remains. The fauna is briefly summarised by SCHAEFFER & PATTERSON (1984, Table 3). In addition to the taxa listed by SCHAEFFER & PATTERSON, there is a number of specimens of a new selachian genus, to be described in a subsequent paper. The purpose of the present work is to describe a single specimen of a new palaeospinacid shark from Osteno (cited as *Hybodus* in SCHAEFFER & PATTERSON 1984: Table 3).

2. - Systematic palaeontology.

Superclass CHONDRICHTHYES, Class SELACHII

Cohort Neoselachii, Order *incertae sedis*

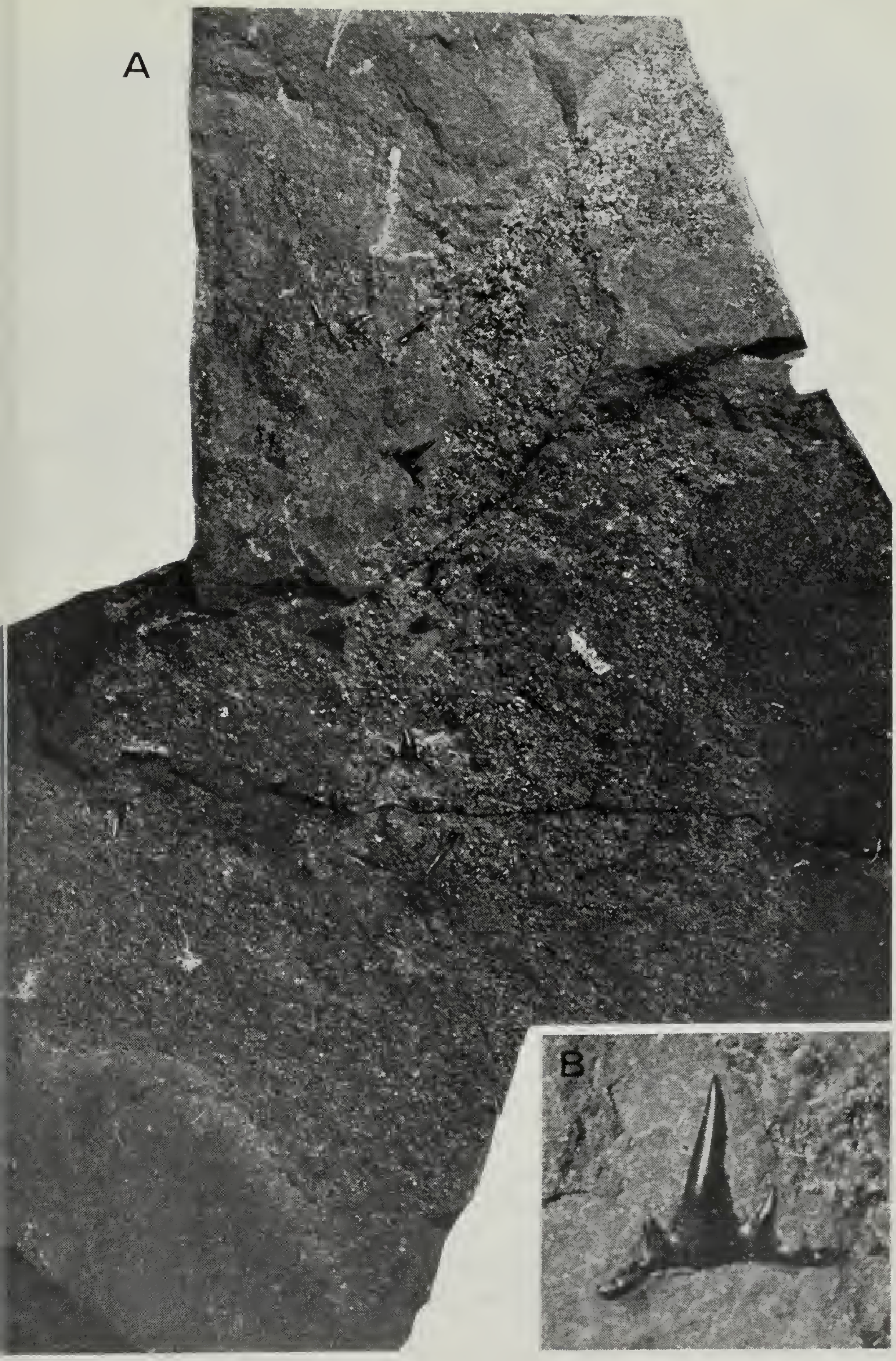
Family Palaeospinacidae Regan, 1906, Genus *Palaeospinax* Egerton, 1872

Palaeospinax pinnai sp. nov.

(Figs. 1-5)

Derivation of name: in honour of Professor Giovanni Pinna (Milan) in recognition of his work on the Osteno fauna.

Fig. 1. — A, *Palaeospinax pinnai*, greater part of the specimen (block 1), × 1; B (inset) detail of a tooth crown in labial view from the same specimen, × 6.


A
B

Diagnosis.

A palaeospinacid shark known on the basis of associated teeth and dermal denticles. The teeth measure up to 7 mm in length, possessing a high, slim central cusp with well developed cutting edges. Up to two pairs of lateral cusplets may be present. Coronal ornamentation is restricted to a pair of short, fine vertical striations on the labial faces of the lateral cusplets. These striations do not bifurcate and terminate well below the cusplet apex. The swollen base of the central cusp overlaps the crown/root junction. The root vascularisation is anaulacorhizoid.

Holotype: V644, Palaeontology Department, Museo civico di storia naturale, Milano. A single specimen in four contiguous pieces and including parts of the dentition and squamation.

Referred specimen: V636, a fragmentary isolated tooth showing very little detail.

Locality: Osteno, eastern shore of Lake Lugano, Como Province, Lombardy, northern Italy. Topographic map: Foglio Valsolda 17 III S.O., Longitude 0. 3° 36′ E, Latitude N. 46° 00′ 40″.

Horizon: spongolithic micrite, Lombardische Kieselkalk Formation, *bucklandi* zone, Lower Sinemurian, Lower Jurassic.

Description.

The specimen is fragmentary and preserves only associated teeth and skin on four rock pieces. The largest two of these pieces (henceforward referred to as blocks 1 and 2) are obviously part and counterpart respectively. Block 2 has been prepared by washing lightly with 5% formic acid in order to loosen and remove sediment adjacent to the teeth and dermal denticles, allowing clearer appreciation of their detailed structure.

Teeth.

A maximum of 23 teeth is represented on the blocks. The bulk of these are broken teeth (10) or impressions (10), yielding little useful information. Six moderately complete teeth and impressions are present and form the basis of this description. The best of these is preserved on block 2 and illustrated in Figure 2.

The tooth is preserved in labial view, and measures 7 mm mesiodistally and 5.2 mm high (root base to cusp apex). The crown bears a high, slim central cusp with well developed cutting edges afforded by

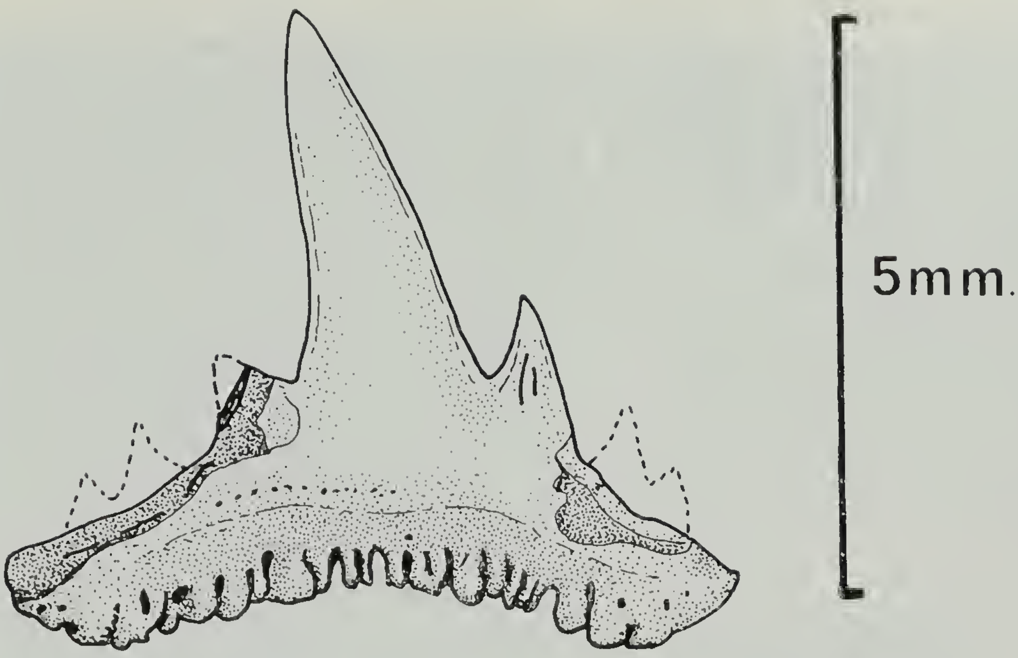


Fig. 2. — Tooth of *Palaeospinax pinnai* as exposed on block 2, in labial view, × 12.

a strong occlusal crest. The central cusp is slightly inclined distally and curves lingually toward the apex. One pair of well developed lateral cusplets is present on the tooth, although the corresponding impression on block 1 indicates that a second and third upright pair were also present originally. The cusplets of the first lateral pair are each 1 mm high, slim in shape with a sharply pointed apex and well developed occlusal crest. The second lateral cusplet pair is approximately half the height of the first pair. The third lateral cusplet pair is rudimentary. Both second and third lateral cusplets are represented by broken bases only on the tooth itself. The crown lacks ornament, with the exception of two very fine vertical striations which ascend the lateral cusplets from a point some way above the cusplet base. These vertical striations do not bifurcate, and terminate well before the cusplet apex.

The central cusp has a swollen base which overlaps the crown/root junction. The same is true for the lateral cusplets, although in these the swelling is less well developed. The crown base terminates against a lip-like development of the labial root wall. The crown/root junction is marked by a series of minute undulations on the upper surface of the labial root wall lip, and is arched beneath the central cusp.

The root is less than one third of the depth of the principal cusp centrally, and shallows mesially and distally. It extends beyond the mesial and distal limits of the crown. The mesial and distal root extensions have convex upper surfaces leading toward the crown/root junction.

Centrally, the labial root face is considerably inclined lingually beneath the principal cusp, forming a marked root sulcus (JOHNSON 1981).

The root vascularisation is anaulacorhizoid (*sensu* CASIER 1947). Entrant vascular foramina are all restricted to the base of the labial root face. The foramina are large and simple in outline, forming an essentially single row close to the junction of the basal and labial faces of the root. The foramina enter the root at a variety of angles, from sub-horizontal to steeply inclined. The blood vessels entering the root would have risen steeply to a vertical orientation after punctuating the labial root face in virtually all cases. The partitions between the vascular foramina have a pillar-like appearance with club-like, spatulate bases. No details of the lingual side of the tooth are available for study.

Variation.

The remaining teeth in the specimen vary from 4 to 6 mm in length (mesiodistally). From those teeth and impressions in which the crown can be discerned, it appears that very little heterodonty is present. The majority of the teeth have an upright central cusp, rather than inclined as in that described above. The central cusp varies from vertical to approximately 30° from the vertical distally. The lateral cusplets occur in three pairs flanking the central cusp, and consistently bear two light vertical striations on the labial face. These striations are also present on the second and third lateral cusplet pairs in some teeth. The lateral cusplets may be rather more robust than in the tooth described above. From broken teeth it can be observed that the crown is orthodont, and that the vascular foramina lead into canals which converge beneath the central cusp. The lingual face of the root is partially visible in one tooth and carries a row of simple vascular foramina along the base of the lingual face of the root. The root is consistently lingually displaced beneath the crown.

There is insufficient information available from the teeth preserved in the specimen to give a characterisation of the heterodonty, or to identify from which jaw the teeth are derived.

Enameloid ultrastructure.

A small section was removed from the central cusp of one of the teeth and etched in 2M HCl for 3 seconds to reveal details of the ultrastructural anatomy of the enameloid. The tooth fragment was studied with S4-10 and S100 Cambridge Instruments scanning electron microscopes (SEM), using an acceleration voltage of 5 KV. The results are shown in Figure 3. The transverse fracture of the central cusp clearly

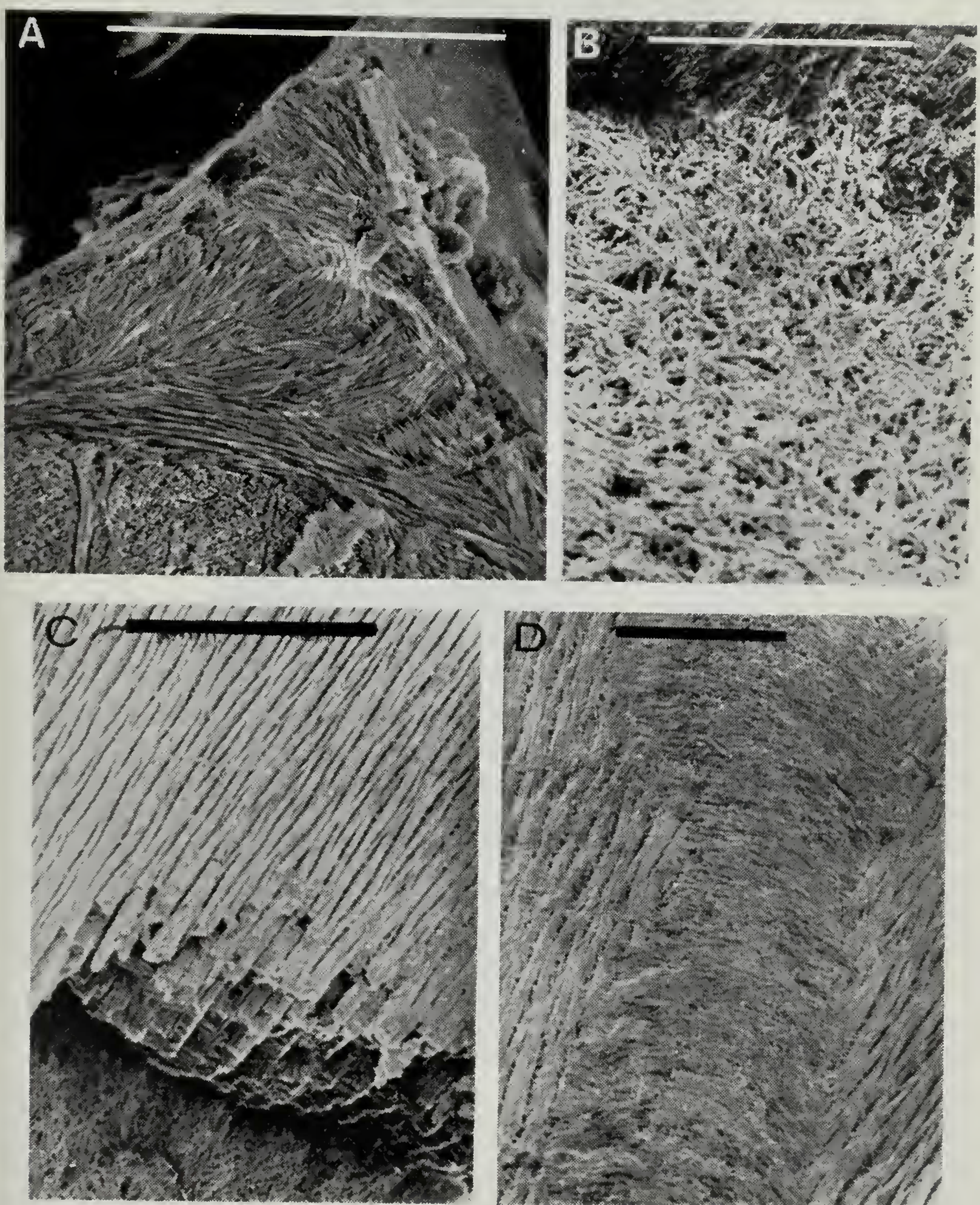


Fig. 3. — A, Etched fracture surface on the central cusp of a tooth of *Palaeospinax pinnai* at the occlusal crest, bar scale = 100 μm; B, detail of the basal layer of tangled fibred enameloid, bar scale = 50 μm; C, detail of the parallel fibred enameloid, bar scale = 100 μm; D, detail of the parallel fibred enameloid at the occlusal crest in surface view, bar scale = 50 μm.

shows an enameloid layer which is at its thickest (40 μm) at the cutting edges (Figure 3A), where the occlusal crest runs down the sides of the cusp. The overall arrangement of the enameloid layer conforms to that of the Toarcian (Lower Jurassic) palaeospinacid described by Reif (1974).

As in the bulk of the neoselachian sharks, the enameloid of *P. pinnai* is triple-layered, comprising a basal layer of tangled fibres (Figure 3B), surmounted by a parallel-fibred layer (Figure 3C), which is overlain in turn by a surface layer of shiny enameloid. The occlusal crest, forming the cutting edge of the tooth, is crossed by a series of fine fibres oriented transversely within the parallel-fibred enameloid layer (Figure 3D).

Dermal denticles.

Associated with the teeth on the micrite blocks is a quantity of skin retaining the shagreen. On block 1 an area of some 50 cm of skin is represented. The dermal denticles show a variety of shapes, sizes and orientations. Unfortunately, the skin patches have proved of little assistance in judging the orientation and aspect of the specimen as a whole. No evidence of prismatic cartilage tesserae is present underneath or in association with the dermal denticles and teeth, so far as can be seen. The teeth, like the dermal denticles, have various orientations and are preserved in several views. The skin surrounds the teeth to a greater or lesser extent on all sides, and no limits of a rostrum or jaw margin can be discerned. Some of the dermal denticles are exposed in surface view, while others are exposed in basal and various oblique views. The denticles tend to be clustered in small articulated groups of up to about 20. Complex folds in the skin, now supported by the matrix, are visible in some areas of the block, especially in the area of the tooth illustrated in Figure 2 and described in detail above. In some areas, the denticles form a jumbled mass, while in others several denticle groups may be superimposed upon each other. In general, block 2 exposes denticle crowns in surface view, and block 1 preserves corresponding impressions or denticles in basal view. Many reversals of orientation are present over the block surfaces, however, presumably representing complex skin folds further disrupted and complicated by compaction. Although several denticle types are represented, they tend to occur in distinct groups with little traceable gradation between. However, the denticle types can be placed into a gradually changing sequence when groups from different areas of the block are compared.

Because of the difficulties in identification of the general orientation and aspect of the specimen as a whole, it is impossible to estimate the scale sources in relation to overall body morphology, or to give a

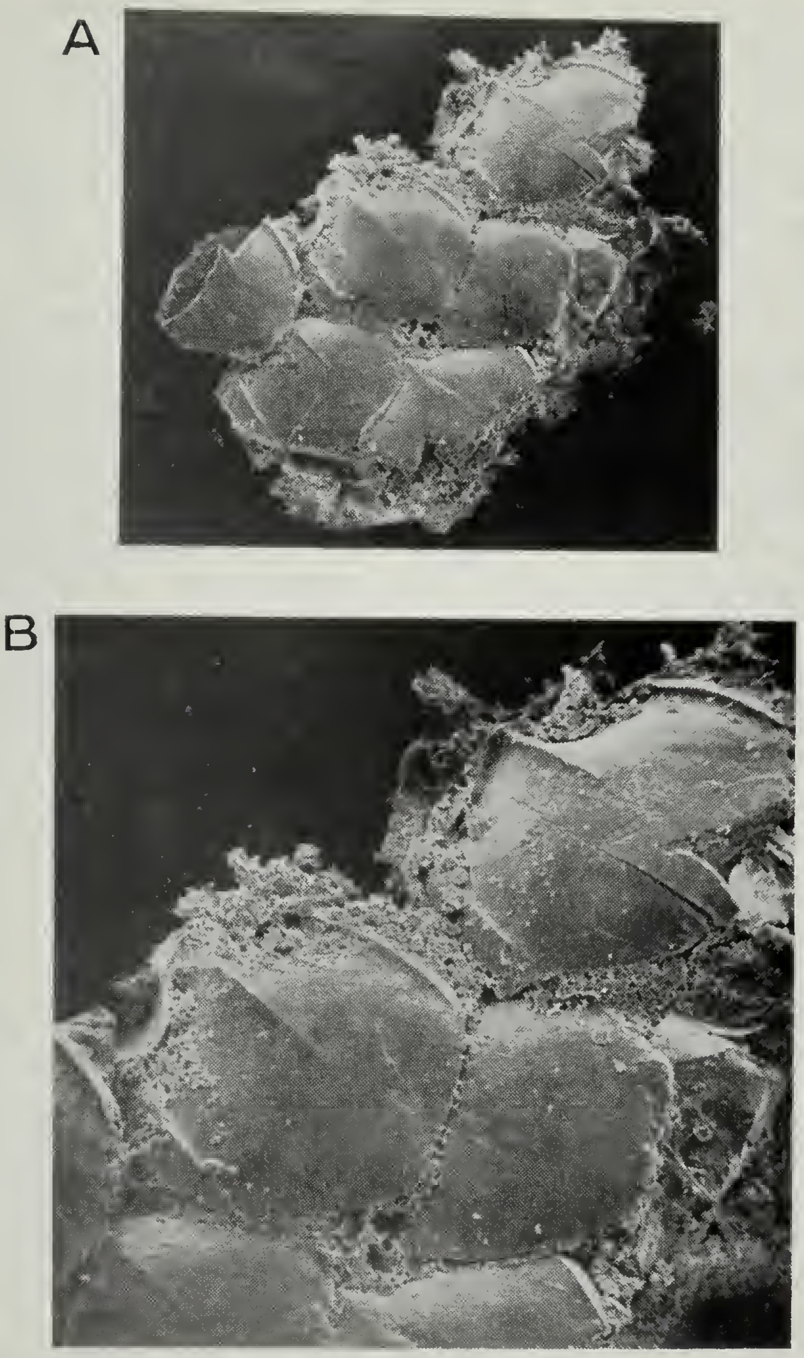


Fig. 4. — A, group of scales of *Palaeospinax pinnai* in surface view, × 100; B, higher power view of the same specimen to show antemortem scratches, × 200.

worthwhile opinion on the taphonomic effects upon the skin of the carcass of postmortem and post-depositional factors. Since the teeth show fairly close association, although disarticulated, it must be presumed that little displacement has occurred in the fossil. Therefore, the bulk of the dermal denticles must presumably derive from the head region of the animal.

The range of dermal denticle morphology is illustrated by SEM photographs of complete scales in Figure 4, and outline drawings of the crown shape of *in situ* scales in Figure 5. All of the scales are simple and non-growing. They fall into two rough size groupings; the majority are very small scales averaging around 0.5 mm across the crown, while rarer, larger scales may reach 1.0 mm. In the smaller scales, the tetraradiate base flares outward from the short pedicel and is generally ornamented by a series of fine, radial ridges. The generally flat basal face of the basal plate possesses a single central vascular foramen. The pedicel is generally unornamented, the radial ridges on the surface of the basal plate terminating just above the pedicel basal plate junction. The crown is spatulate in the majority of denticles, conforming to the « placoid » morphotype of Reif (1978). The spatulate crowns vary between 0.3 and 0.6 mm across their widest point in surface view. The posterior tip of the crown may be sharply pointed or rounded. The overall crown shape in surface view may be subrounded to laterally expanded. A longitudinal ridge is developed around the anterior margin of the crown and may extend round the lateral and posterior borders also. This ridge may be smooth, undulating or crenulate. The anterior margin of the crown may be smooth or invaginated with sulci separating a central keel from two lateral keels (Figures 4A, B). The keels may bear fine vertical striations arising from the longitudinal ridge. Up to three vertical striations may be developed on the central keel. These may be very short, or extend all the way to the crown apex, and may coalesce after a short distance in some cases. A small node may be developed at the junction of the vertical and longitudinal striations on the central keel in some specimens. The lateral keels are often upturned and bear up to two vertical ridges. The central keel is always the most prominent. Most of the crowns are transparent and reveal a fine, fan-like network of dentine tubules beneath the enameloid.

The larger denticles measure up to 1 mm across the widest point of the crown surface. The crown in these forms is much more robust, lacking the spatulate shape of the smaller crowns and not produced posteriorly. The pedicel is short, the basal plate not so flared as in the smaller crowns, and the crown sits directly on the top of the pedicel. These larger crowns may have very short vertical ridges, if developed at all. The central and lateral keels are absent producing a more circular and domed outline. The crowns are mostly subrounded in surface view. The longitudinal ridge surrounds the entire crown, but is finer and less crenulate that in spatulate crowns.

Denticles of both types may show signs of antemortem wear on the crown surface (Fig. 4B). Elongate scratch marks produced by antemortem

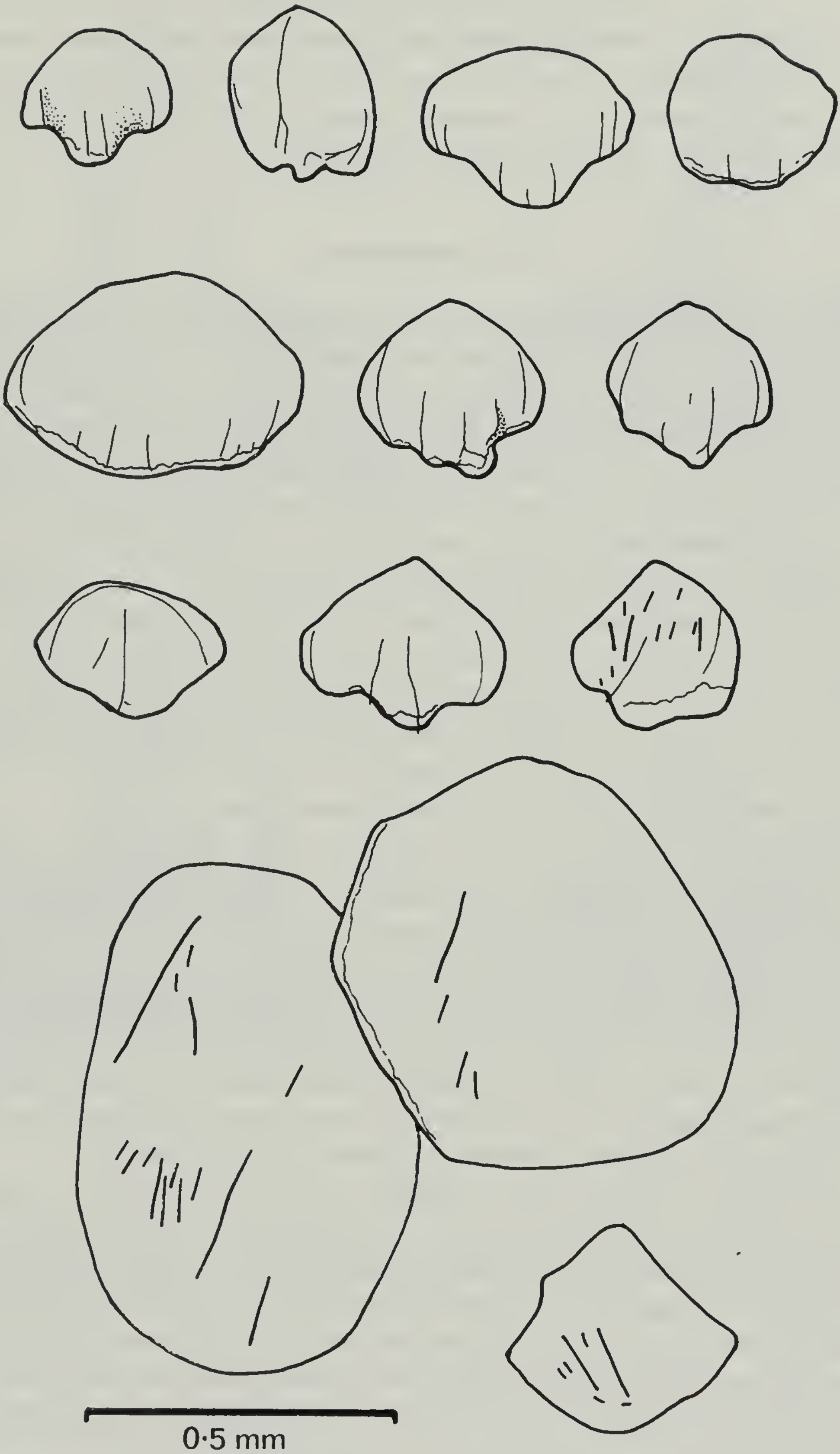


Fig. 5. — Outline drawings of scale types of *Palaeospinax pinnai* drawn from V644, blocks 1 and 2. Note the presence of antemortem wear scratches on the larger, and the lower two of the smaller scales.

abrasion may be quite deep and cross the greater part of the crown diameter (Fig. 5). Numerous finer and shorter scratches often accompany these isolated larger striae. The majority of the scratches is aligned roughly anteroposteriorly in spatulate crowns, and tend to show constant orientations in the crowns of larger denticles.

3. - Discussion.

The palaeospinacid sharks were first established by the description of *P. priscus* Egerton (1872) from the Lower Liassic (Sinemurian, Lower Jurassic) of Lyme Regis, on the Dorset coast of southern England (Agassiz 1843; Egerton 1872). Woodward subsequently (1889) described *P. egertoni* from the Posidonienschiefer (Toarcian, Lower Jurassic) of Baden Wurttemberg, south-west Germany, from which a later record of the genus was recently made by Reif (1974). *P. priscus*, the type species, is now known by several specimens of varying size and completeness (Davis 1881; Woodward 1889; Dean 1909). *Palaeospinax* was reviewed by Maisey (1977), and additional species described by Duffin (1982) (*P. rhaeticus* from the British Upper Triassic) and Thies (1983) (*P. kruckowi* and *P. riegrafi* from the Aalenian and Oxfordian respectively of Germany). Duffin and Ward (in prep.) are currently preparing a revision of the palaeospinacid sharks and their close allies.

Palaeospinax has become established in the literature as belonging to one of the most primitive neoselachian shark lineages. Neoselachian sharks are those which, broadly speaking, show character associations typical of the extant shark families. The record of an isolated tooth closely resembling those of *Palaeospinax* from the Scythian (Lower Triassic) of Turkey (Thies 1982) suggests that it is part of a very ancient neoselachian lineage. The only known neoselachian predecessors of the palaeospinacids are the anachronistid sharks from the British and American Carboniferous and Permian (Duffin & Ward 1983).

In his classic paper on the grades of selachian evolution, Schaeffer (1967) concluded that *Palaeospinax* was the oldest and most primitive member of the modern level sharks. Maisey (1975, 1977) concluded that *Palaeospinax* bridged the morphological gap between the ctenacanthids and neoselachians, primarily on the basis of fin spine histology. *Palaeospinax* has been used as an example of a neoselachian lying close to the ancestral morphotype (Compagno 1977; Schaeffer & Williams 1977; Thies 1983).

As can be seen from the brief outline given above, *Palaeospinax* has assumed an important position in discussions bearing on neoselachian

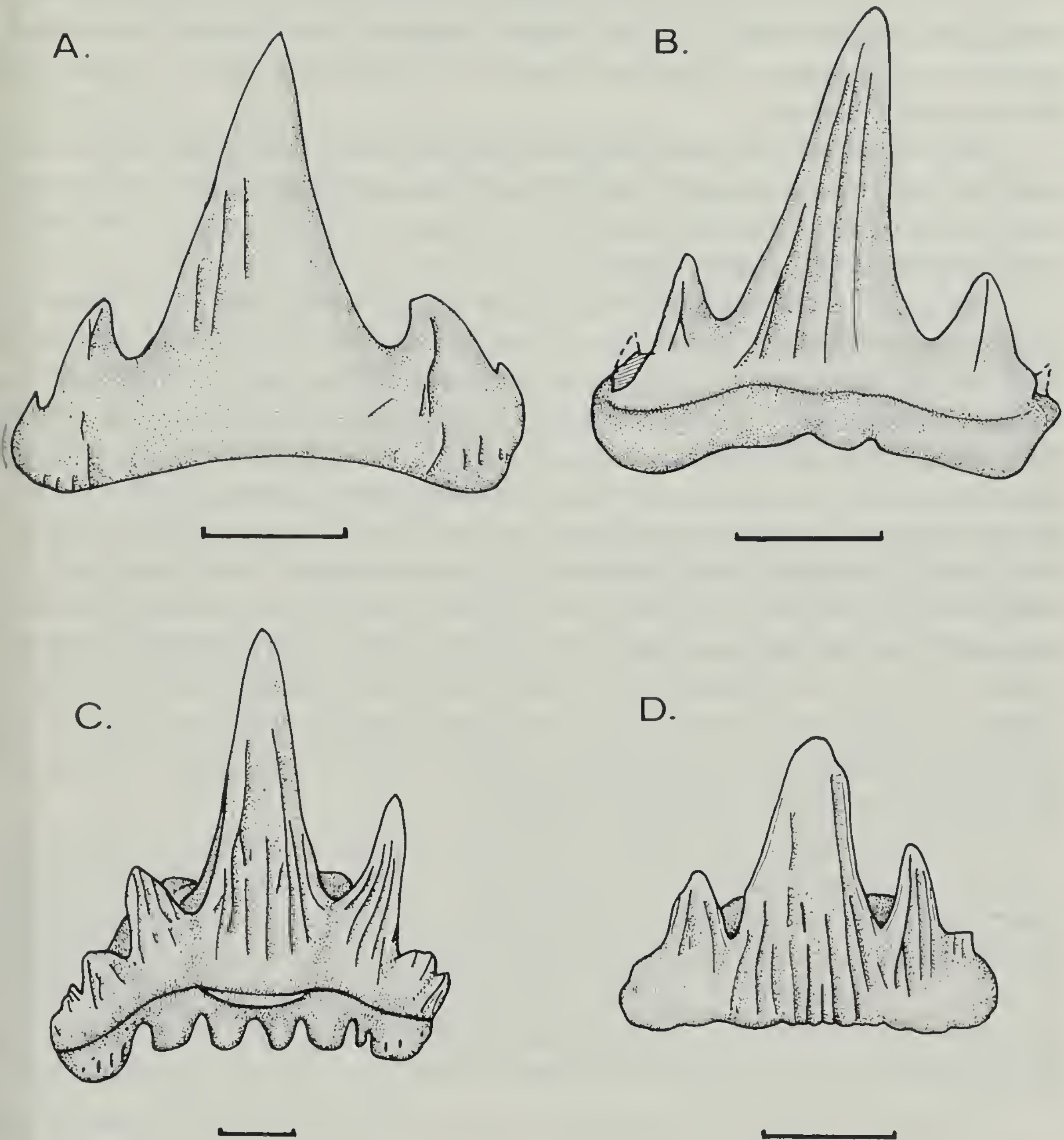


Fig. 6. — Palaeospinacid sharks teeth in labial views. A, upper anterolateral (possibly even symphyseal) tooth of *Palaeospinax egertoni* Woodward (1889), drawn from BM (NH) P.1132 (Holotype), Toarcian (Lower Jurassic) of Ohmden, near Holzmaden in south-west Germany; B, upper symphyseal tooth of *Palaeospinax priscus* Egerton (1872), drawn from BM (NH) P.3189, Sinemurian (Lower Jurassic) of Lyme Regis, Dorset, southern England; C, Holotype of *Palaeospinax kruckowi* Thies (1983), SMF 7096, drawn from Thies (1983 pl. 2 fig. 1a). The specimen is from the Upper Aalenian (Upper Jurassic) of Moorberg in northern Germany; D, Tooth of *Palaeospinax riegrafi* Thies (1983), SMF 7099, from the Upper Oxfordian (Upper Jurassic) of Buchsteige in southern Germany. Bar scale = 1 mm in all cases.

ancestry and relationships. The fossil record of the genus is based primarily upon isolated teeth and fin spines, together with some articulated partial and complete skeletons from the Sinemurian and Toarcian of Britain and Germany.

The record of *Palaeospinax pinnai* from the Sinemurian of Osteno adds to the known diversity of the early neoselachians, and extends the known palaeogeographical range of the genus from Britain, Germany and Turkey into northern Italy.

The teeth of *Palaeospinax* are superficially quite similar to those of certain contemporary hybodont sharks, in that the crown and root are not sharply demarcated, and in the anaulacorhize root vascularisation (*sensu* CASIER 1947; DUFFIN & WARD 1983). The root is lingually offset from the crown, and does not possess the V-shaped basal face which is more typical of neoselachian teeth (DUFFIN 1980; THIES 1983). Neoselachian sharks usually possess roots which have a restricted and specialised vascularisation, while the teeth of *Palaeospinax* have multiforaminate roots, in which the individual vascular canals are largely indiscriminately distributed over the whole root surface. Palaeospinacid roots share a unique vascularisation on the labial root face, however. Canals enter the labial root wall at a very steep angle giving rise to vertical intervening pillars of root tissue. In labial view the root has a furrowed appearance along the basal root margin.

This character is strongly developed in *P. pinnai* (Fig. 2) and testifies to its palaeospinacid affinities. The presence of a triple-layered enameloid closely resembling that described for *Palaeospinax* sp. by REIF (1974) strengthens this conclusion. The scales are simple and non-growing, as seen in neoselachians, and also post-Rhaetian hybodonts (REIF 1978). A detailed comparison of scale morphologies between the various species of *Palaeospinax* will be made elsewhere (DUFFIN & WARD, in preparation).

P. pinnai can best be compared to other palaeospinacid sharks using dental characters, although a full dentition and characterisation of heterodonty for the Italian species is wanting.

The teeth of *P. pinnai* bear a high, upright central principal cusp flanked by three lateral cusplet pairs. The crown ornament is restricted to fine vertical striation pairs on the lateral cusplets only. At over 5 mm high, these teeth are quite large.

The teeth of *Palaeospinax* sp. from the Lower Triassic of Turkey (Thies 1982) are much smaller (less than 1 mm high), and known only from a single fragmentary crown. A series of fine vertical striations is visible ascending the labial face of the central cusp (Thies 1982, fig. 2a) and there is a single preserved lateral cusplet. A horizontal striation is present toward the base of the central cusp and lateral cusplet, from which certain of the vertical striations arise. There is no horizontal striation in *P. pinnai,* and the vertical ornament is much reduced by comparison.

Teeth have not, as yet, been described for *P. rhaeticus,* which was described from fin spines from the British Upper Triassic (DUFFIN 1982). The next record of the genus is *P. priscus* from sediments broadly contemporaneous with those yielding the Osteno fauna (Sinemurian, Lower Jurassic). *P. priscus* is known from complete and articulated material, including well preserved dentitions. In spite of this, the teeth have never been described in any detail and with respect to heterodonty, although they have been illustrated on several occasions (eg. EGERTON 1872 pl. 7; MAISEY 1977 fig. 2). The teeth of *P. priscus* (Fig. 6B) are unlike those of *P. pinnai* in that they possess long, coarse vertical striations over the whole of the crown. Three lateral cusplet pairs may be present in lateral teeth, but this is reduced in symphyseals and posterolaterals. The central cusp decreases in height posteriorly through the dentition, such that the posterolateral teeth are very low-crowned indeed. The teeth of *P. priscus* are approximately half the size of those in *P. pinnai.*

P. egertoni, from the German Toarcian (Lower Jurassic) is known from two specimens, only one of which preserves parts of the dentition. The teeth (Fig. 6A) are of comparable size to those described for *P. pinnai,* but possess a central cusp which is much more squat and robust. To illustrate this point, the dimensions of central cusp height, divided the mesiodistal length of the central cusp base can be expresed as an index. In teeth of *P. pinnai,* the index produced varies between 2.1 and 2.2, whereas in teeth of *P. egertoni* it is 1.38.

Vertical striations vary in their development on teeth of the German species, but when present are much coarser than those encountered on *P. pinnai.*

The specimen described as *P. egertoni* from the Posidonienschiefer by REIF (1974) belongs to a new species. The material is currently being described by Dr. Detlev Thies of Hannover. It is obvious from Reif's figures (REIF 1974 fig. 3b-d) that the teeth of this species are unique in possessing up to five lateral cusplet pairs. Also, the central cusp is not as slender as in *P. pinnai,* having a cusp height to cusp base ratio varying from 1.6 (in symphyseal teeth) to 1.1 (in posterolateral teeth), as compared to an average of 2.15 in *P. pinnai.*

THIES (1983) described *P. kruckowi* from two isolated teeth from the Aalenian (Middle Jurassic) of northern Germany. Of comparable size to the teeth of *P. pinnai,* those of *P. kruckowi* (Fig. 6C) show coarser and more widespread coronal ornament. The central cusp and up to three lateral cusplet pairs are quite slender, and all bear vertical striations, which may attain the occlusal crest and often show coalescence, in contrast to the Italian material. The central cusp height to base length ratio is 2.27 in *P. kruckowi*, comparing quite closely with the figure of 2.1 to 2.2 for *P. pinnai*.

P. riegrafi Thies is known from ten isolated teeth from the Upper Jurassic) of southern Germany. Half the size of those of *P. pinnai*, the teeth of *P. riegrafi* also differ in the extreme lingual inclination of the crown, and presence of very coarse vertical striations (Fig. 6D).

4. - Conclusions.

From the above discussion, it is obvious that *Palaeospinax pinnai*, described on the basis of 1 partial specimen from the Sinemurian of Italy, is a new palaeospinacid shark. Its dentition differs from all previously described members of the genus in tooth size and outline, and in the rather restricted coronal ornament. Palaeospinax is no longer restricted to the Germano-British Basin, but is also known to be present in the Tethyan area, as the Osteno record confirms.

Acknowledgements. — It is a pleasure to thank my colleagues, Professors Pinna and Teruzzi for permission to work on the material. The manuscript was critically read by Prof. G. Pinna, Dr. C. Patterson and Mr. D. Ward, to whom my thanks are extended.

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